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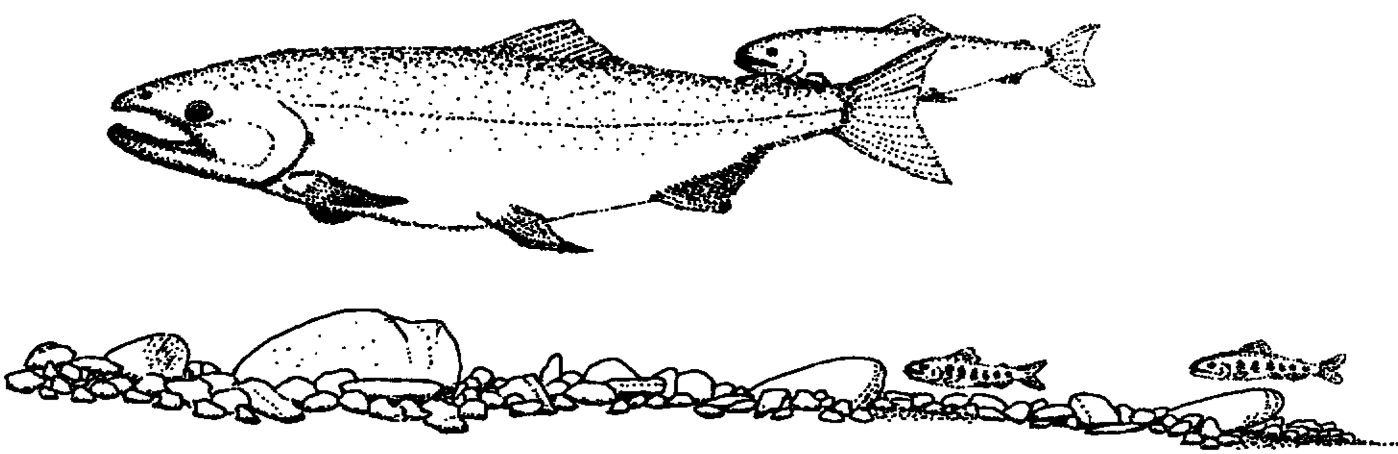
MICROHABITAT SELECTION AND BEHAVIOR OF SUMMER REARING JUVENILE COHO SALMON IN THE MAINSTEM CLEARWATER RIVER, WASHINGTON



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Microhabitat Selection and Behavior of Summer Rearing Juvenile Coho Salmon in the Mainstem Clearwater River, Washington

by

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ABSTRACT

We evaluated the microhabitat distribution and behavior of summer rearing juvenile coho salmon (*Oncorhynchus kisutch*) in the mainstem Clearwater River. Two distinct foraging behavior classifications (foraging and resting) were observed in juvenile coho salmon rearing in the mainstem Clearwater River. Foraging coho salmon were active foragers, while resting fish generally displayed little foraging or social behavior. Foraging and resting coho salmon showed differences in habitat use and intensity of foraging and agonistic behaviors. Foraging coho salmon occupied faster focal current velocities (0.07 m/s) than resting coho salmon (0.004 m/s) and generally selected focal positions in deeper water and were deeper in the water column than resting coho salmon. Coho salmon in the mainstem Clearwater river usually were not directly under woody debris cover. Distance from woody debris varied with behavior classification and habitat type. Foraging coho salmon were farther from woody debris cover than resting coho salmon in glides, while resting coho salmon were farther from woody debris cover than foraging coho salmon in riffles. Foraging juvenile coho salmon displayed more aggressive and submissive behavior than resting fish. Somewhat limited data suggest substantial exchange of coho salmon between foraging and resting behaviors. Results emphasize the importance of conducting habitat use evaluations at whatever scales are most appropriate and are discussed with reference to habitat enhancement/restoration of larger, mainstem rivers for juvenile coho salmon rearing.

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INTRODUCTION

A number of studies have described the behavior and microhabitat distribution of juvenile coho salmon (*Oncorhynchus kisutch*) in small streams (for example, Chapman 1966; Chapman and Bjornn 1969; Nielsen 1992). In contrast, little is known about the microhabitat distribution and behavior of juvenile coho salmon in larger streams (4^{th} order and larger). Significant differences in microhabitat distribution and behavior may occur as stream size increases.

Several factors associated with increasing stream size may influence habitat use by juvenile salmonids, including the increase in channel size (Baltz and Moyle 1984). The factors associated with increased channel size that could influence microhabitat use by salmonids include: differences in fish community structure (Beecher et al. 1988), predators and competitors (Fausch and White 1981; Baltz et al. 1982; Bugert and Bjornn 1991; Schlosser 1987; Tabor and Wurtsbaugh 1991), temperatures (Baltz et al. 1982; Reeves et al. 1987), food availability (Wilzbach 1985), fish size (Dolloff and Reeves 1990), and behavior (Nielsen 1992, 1994). Recent emphasis on rehabilitation of stream habitat, including that of larger rivers, requires a better understanding of habitat selection and behavior of salmonids in these larger systems.

Nielsen (1992, 1994) observed differential habitat use by juvenile coho salmon displaying distinct foraging behaviors in Washington and California streams and concluded that these foraging groups developed in response to environmental factors. Therefore, different foraging behaviors may occur in large rivers, which possess distinctly different physical environmental conditions from those of small streams. Swain and Holtby (1989) observed differences in agonistic behavior between juvenile coho salmon rearing in a lake and its inlet stream. Also, the body form of lake rearing coho salmon, more streamlined and smaller less colorful fins, appeared to be better suited for schooling in open water than for stream rearing. Juvenile coho salmon displaying the foraging behaviors described by Nielsen (1992, 1994) and those displaying schooling behaviors would likely use different microhabitats. If these (or other) foraging behaviors are observed in juvenile coho salmon from large rivers, habitat enhancement measures should attempt to provide habitats important for fish displaying each behavior. Different foraging behaviors may segregate available resources and allow greater densities of the species to occur in available habitat. Therefore, the most successful habitat restoration programs should be those providing adequate rearing conditions for the greatest number of behavioral groups.

The purpose of this study was to evaluate microhabitat use and behavior of summer rearing juvenile coho salmon in a relatively large stream channel and determine if woody debris introductions are adequate to provide rearing habitat for different behavioral groups which may be observed. For the purpose of this study, microhabitat has been defined as the habitat characteristics associated with the focal position of individual fish.

Study Area

This study was completed in the mainstem Clearwater River. The Clearwater River originates from the west slope of the Olympic Mountains, flows west to southwest for 58 km to its confluence with the Queets River (Winter 1992). The river's drainage area of approximately 350 km^2 (Cederholm and Scarlett 1982) receives over 350 cm of rain annually (Cederholm and Scarlett 1991). The river is fed primarily by surface runoff and ground water (Winter 1992). Median discharge near the town of Clearwater for the years 1932 and 1938-1949 ranged from about 3.7 m^3/s to 9.3 m^3/s from June to September; a peak flood of 1,059 m^3/s was recorded 3 November 1955 (Amerman and Orsborn 1987). The river gradient is low to moderate and the river is composed primarily of pools with relatively short riffles (Phinney and Bucknell 1975).

During 1992, four debris accumulations between Deception Creek and Peterson Creek were selected for microhabitat study (Figure 1). During 1993, 19 debris accumulations were selected. Six of these accumulations were located between Bull and Deception creeks, eleven were between Peterson Creek and Gross Bridge, and two were between Elkhorn and Hunt creeks (Figure 1).

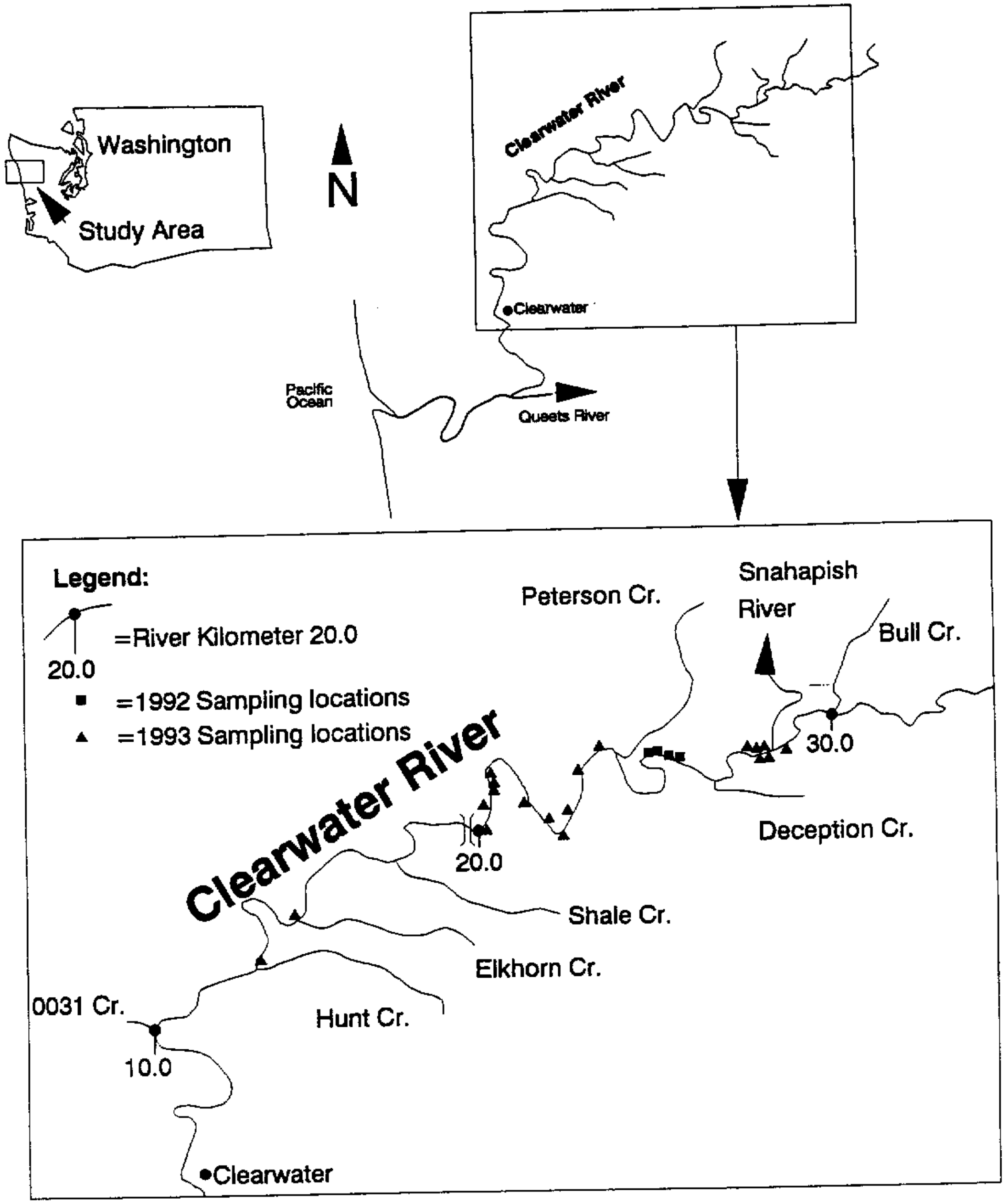

Figure 1. Study reaches of the mainstem Clearwater River where microhabitat selection and behavior of juvenile coho salmon was evaluated during 1992 and 1993.

MATERIALS AND METHODS

Habitat Use and Behavior

1992

Preliminary observations of microhabitat use and behavior were collected during 1992 near four woody debris accumulations of the mainstem Clearwater River. Three of these accumulations were introduced woody debris and one was natural. Juvenile coho salmon at these debris accumulations were observed by snorkeling during four distinct periods (early and late August, late September, and early October). A snorkeler entered the water downstream (at least 10 meters) of the debris accumulation and proceeded upstream until a group of coho salmon was observed. A 5-min adjustment period, with the snorkeler waiting quietly in the water, proceeded collection of behavioral data. Following the acclimation period, the group was classified as either foraging or resting (Table 1) and the number of juvenile coho salmon in the group was estimated. A randomly selected individual fish was then observed and classified as either dominant, subdominant, or as a floater if it was in a foraging group (Table 1). Fish from the resting group were not further classified. The number of foraging attempts and behavioral displays (Table 2) made by the individual fish during a 2-min observation period were recorded underwater. Additional randomly selected juvenile coho salmon were observed until at least 20% of the fish in the group had been observed. The snorkeler then proceeded until another group was found, after which the process was repeated. Following the completion of all behavioral observations, microhabitat variables, including focal velocity, water depth, focal depth, distance from bottom, relative depth (calculated by dividing focal depth by water depth), and distance from woody debris were measured for each group observed (Table 3). Several measurements for each variable were taken over the entire area used by the group.

Habitat use and behavioral observation data were collected by two individuals during 1992. These individuals observed different groups of fish at different debris stations simultaneously to increase the number of fish which could be observed during the study. Habitat use and behavioral data collected by these two individuals were compared using separate t-tests for juvenile coho salmon from the foraging and resting behavior groups. If significant differences existed between observers, subsequent analysis of variables for which significant differences existed were completed separately for each observer.

Table 1. Definitions of terms used to classify behavioral groups and individual coho salmon rearing at debris accumulations in the mainstem Clearwater River. (Adapted and modified from Puckett and Dill (1985)).

	Definition
Resting	A group of fish not actively feeding or displaying other activities (wandering, schooling, etc.).
Foraging	A group of fish actively pursuing food items.
Dominant	Individual fish at the most upstream position of a foraging hierarchy or aggregate.
Subdominant	Individual fish within a foraging hierarchy or aggregate but not at the most upstream position.
Floater	Individual fish foraging in a foraging arena, not associated with a foraging social hierarchy (Puckett and Dill 1985).

Table 2. Definitions of foraging and social behaviors recorded for individual juvenile coho salmon rearing at woody debris accumulations in the mainstem Clearwater River (Adapted from Kalleberg (1958)).

Behavior	Definition
Foraging	
Surface	Breaking the water surface to obtain a food item.
Mid-Water	Foraging on suspended food items within the water column.
Benthic	Making contact with the substrate while feeding.
Wandering	Continuous undirected swimming.
Aggressive	
Display	Flaring of fins and assumption of the tilted posture with the aggressor's head lowered toward the opponent.
Attack	Rapid swimming toward another fish without direct contact.
Nip	Biting movements by the aggressor towards another fish.
Chase	Chasing another individual as it flees from the attack.
Submissive	
Belly Display	Showing of the belly resulting in broken eye contact between the aggressor and submissive fish.
Flight	Fleeing from an attack.
Hiding	Using cover to evade an attack.

Table 3. Definitions of physical habitat variables measured to describe microhabitat selection of juvenile coho salmon in the mainstem Clearwater River.

Habitat Variable	Definition
Focal Velocity	Water velocity (m/s) at the fish's snout.
Depth	Perpendicular distance (m) from the substrate to the surface of the water measured at the snout of the fish.
Focal Depth	Perpendicular distance (m) from the fish's snout to the water surface.
Distance From Bottom	Perpendicular distance (m) from the fish's snout to the substrate.
Relative Depth	Focal Depth/Water Depth.
Distance to (from) woody debris	Horizontal distance (m) from the fish's snout to the nearest woody debris cover.

Habitat use by juvenile coho salmon was compared between behavior groups (resting, foraging) during 1992 using a two-way ANOVA. The time period (early and late August, late September, and early October) during which observations were made was included in the two-way ANOVA as the second factor to determine whether habitat use changed during the survey period. The interaction between behavior group and sampling period also was examined. Statistical analysis of relative depth data was completed using arcsine transformed data ($X' = \arcsin (X)^{1/2}$). Foraging and behavioral data for 1992 were evaluated using a t-test to determine whether differences in these behaviors existed between juvenile coho salmon from the two behavior groups (foraging and resting).

1993

Nineteen stations were included in the evaluation during 1993. Eight were introduced debris accumulations and 11 were natural debris accumulations. Four of the eight introduced debris accumulations were located in pools and four in glides, four of the natural debris accumulations were in pools, four in glides, and three in riffles. Juvenile coho salmon were caught during 1993 with beach and purse seines at each woody debris accumulation. Ten coho salmon were randomly selected from the catch and marked (July 26-August 2, 1993) with non-toxic acrylic paint which was injected into the rays of the dorsal and/or caudal fin. At one station, fourteen coho salmon were marked because of the high abundance at this station ($\approx$400) compared to the others ($\approx$100). Different color combinations and mark locations were used for differential marking of individual fish (Lotrich and Meredith 1974; Thresher and Gronell 1978). Once marking was completed, the fish were released into the area from which they had been taken. Behavioral observations and habitat selection data were collected exclusively on these marked fish during two separate observation periods in 1993. The first set of observations were made between 5 August and 18 August, 1993 and the second between 13 September and 24 September, 1993.

As in 1992, behavioral and habitat selection observations were completed by snorkeling. A snorkeler would enter the water downstream of the debris accumulation to be surveyed, moving upstream until a marked fish was observed. Following a 10-min adjustment period, the group which the marked fish was a member was classified as foraging or resting (Table 1). Behavior activity (Table 2) of the marked fish was then recorded over a 10-min observation period. If the group contained more than one marked individual, behavioral observations for the remaining marked fish occurred following the 10-min observation of the previously observed fish unless the observer had to move to obtain adequate observations. In this case, an additional 10-min adjustment period occurred prior to making behavioral observations. Foraging and behavior data were defined as described above.

Physical habitat variables (same as in 1992) were measured following the observation of all marked fish at a debris station (Table 3). In contrast to 1992, habitat measurements were recorded for individual marked fish for which behavior data was collected rather than the group. Habitat measurements were measured as described for 1992.

A t-test was used to determine whether microhabitat use by juvenile coho salmon in the mainstem Clearwater River differed between August and September, 1993. If no significant differences were detected, data for the two sampling periods were combined for further analyses. However, if significant differences existed, data from each month were analyzed separately. All statistical analyses of relative depth data was completed with arcsine transformed data ($X' = \arcsin (X)^{1/2}$).

A two-way ANOVA was used to compare habitat use by individual marked juvenile coho salmon from the two behavior groups (foraging and resting) and by juvenile coho salmon rearing in different river habitats (pool, glide, riffle). If a significant interaction existed between the two variables, habitat use by juvenile coho salmon from the two behavior groups were compared separately for each type of habitat using a t-test. Statistical test for individual factors are meaningless if the interaction between the terms is significant, therefore, a conservative alpha level (P=0.10) was used to test the interaction (Zar 1984).

The effect of foraging position (dominant, subdominant, floater) and habitat type (pool, glide, riffle) on habitat use by juvenile coho salmon from the foraging group were evaluated using a two-way ANOVA. Because resting fish did not display dominant behavior, a one-way ANOVA was used to evaluate the effect of river habitat (pool, glide, riffle) on habitat use.

The effect of behavior group (foraging and resting) and sampling period (August and September) on the behavioral activity (e.g., forage, aggressive, submissive behavior) of juvenile coho salmon was evaluated using a two-way ANOVA. If a significant interaction was detected, behavioral activity between these two behavior groups was compared separately for each sampling period using a t-test. One-way ANOVAs were used to compare behavioral activity (e.g., foraging, aggressive, submissive behavior) of the individual classifications (dominant, subdominant, floater) of the foraging group.

The effect of debris type (introduced and natural) and river habitat (pool, glide, riffle) on the number of foraging (surface, midwater, bottom), aggressive (display, nip, attack, chase), submissive (display, flee, hide), and wandering behaviors were evaluated using two-way ANOVAs. Behavior data for foraging and resting groups were combined for analysis if no significant difference existed between these two behavioral groups for the variable in question. Otherwise the analysis was completed separately for each behavioral group.

A two-way ANOVA was used to compare the number of forage attempts made by foraging coho salmon at different locations (surface, midwater, bottom) and from different individual classes (dominant, subdominant, and floater). If a significant interaction was detected between these two factors, the mean number of foraging attempts at each foraging location was tested separately for foraging fish from individual classes using an ANOVA. This same approach was used to compare the type of aggressive (display, attack, nip, chase), and submissive (display, flee, hide) behaviors displayed by coho salmon from different individual classes. One-way ANOVAs were used to compare the number of forage attempts made at different foraging locations (surface, midwater, bottom) and the different types of aggressive (display, attack, nip, chase), and submissive (display, flee, hide) behaviors displayed by juvenile coho salmon from the resting group.

Size and Growth

Weights (g) of all juvenile coho salmon marked during 26 July and 2 August 1993 were recorded. Fifteen unmarked coho salmon from each station were also weighed. Following the last behavioral observations in September, attempts were made to capture coho salmon from each station using beach and purse seining. All marked fish captured, along with a sample of unmarked fish sufficient to bring the total sample size up to 25 individuals, were weighed. Weights of coho salmon captured at different types (introduced and natural) of woody debris accumulations and habitats during the marking survey were compared using a nested ANOVA (station nested). A nested ANOVA (stations nested) was used to compare the weights of juvenile coho salmon receiving marks and those not receiving marks because significant differences (ANOVA: $P=0.0001$) in coho salmon weights existed between stations.

Specific growth (% weight increase/day) rates of marked coho salmon recaptured in September were calculated as:

$$\text{Specific Growth Rate} = ((\log_e Y_2 - \text{Log}_e Y_1)/(t_2 - t_1))*100 \qquad \text{Equation 6.1 (Busacker et al. 1990)}$$

where: Y_1 = initial weight (g)

Y_2 = final weight (g)

t_1 = time initial weight was recorded

t_2 = time final weight was recorded

The specific growth rate of marked juvenile coho salmon re-captured at the end of the study from the station where they were marked, were compared between introduced and natural debris accumulations using a t-test. There were insufficient numbers of marked fish recaptured from different habitat type to complete a comparison of growth rates among habitat types.

Stomach samples were collected from marked coho salmon sampled following the September 1993 observations, using pulsed gastric lavage technique (Foster 1977) and preserved in 70% ethanol. In the laboratory, total weight of the sample and weight of individual taxa in the sample were determined. Average weights of stomach contents were pooled by behavioral groups for comparison.

RESULTS

Habitat Selection

1992

Habitat use data collected by the two observers were not significantly different and therefore were combined for statistical analysis (Appendix A). Groups of foraging coho salmon occupied focal position with greater current velocities and which were farther from woody debris cover than resting fish (Figure 2). Foraging and resting coho salmon selected focal positions with similar water depth, focal depth, distance from bottom, or relative depth (Figure 2). Microhabitat use by juvenile coho salmon from the two behavior groups was not different during the four sampling periods in 1992 (early and late August, late September, and early October) for any of the measured habitat selection variables (two-way ANOVA: P=0.3076 to 0.7863).

1993

No significant differences in microhabitat selection existed between August and September for coho salmon in either behavior group (foraging or resting) except that foraging groups were closer (t-test: P=0.0409) to the bottom during September than August (Appendix B). Since no significant differences in microhabitat use of juvenile coho salmon were observed in water depth, focal depth, relative depth, focal velocity, or distance to debris between months, the data for August and September were combined for additional statistical analysis. Distance to the bottom was analyzed separately for each month during which observations were recorded.

Juvenile coho salmon from the foraging group used focal positions with significantly greater velocities, depths, and relative depths than those from the resting group (Table 4). However, coho salmon from the two behavior groups selected focal positions at similar distances from the bottom during September. Focal depth of juvenile coho salmon rearing in pools was significantly deeper than those rearing in glides and riffles and was deeper in glides than riffles (Table 5). Juvenile coho salmon selected focal positions at greater relative depths in riffles than in pools (Table 5). Relative depths of focal positions were not different between riffles and glides or between pools and glides (Table 5). Focal positions in pools were significantly farther from the bottom than those rearing in riffles during September (Table 5). There were no differences in the distance focal positions were from the bottom for fish rearing in pools versus glides or glides versus riffles. Focal velocities selected by juvenile coho salmon rearing in different habitat types were not significantly different.

Foraging and resting coho salmon used focal positions different distances from woody debris and in different water depth (Table 6). The distance focal positions of foraging and resting fish were located from woody debris cover was dependent upon river habitat. Focal positions of foraging fish were farther from woody debris than resting fish in glides. In contrast, resting fish selected focal positions significantly further from woody debris in riffles. There was insufficient replication for comparison in pools. Foraging fish selected focal positions in significantly deeper water in glides and riffles than resting fish. There was insufficient replication for statistical comparisons of water depth used by foraging and resting fish in pools. Juvenile coho salmon selected focal positions at similar distances from the bottom during August (Table 6). Significant interactions existed between the factors behavior group and habitat type for the variable distance to bottom during August (two-way ANOVA: $P=0.0015$), water depth (two-way ANOVA: $P=0.0002$), and distance from debris (two-way ANOVA: $P=0.0001$). Thus, habitat use of resting and foraging groups were compared separately for each habitat type (Table 6).

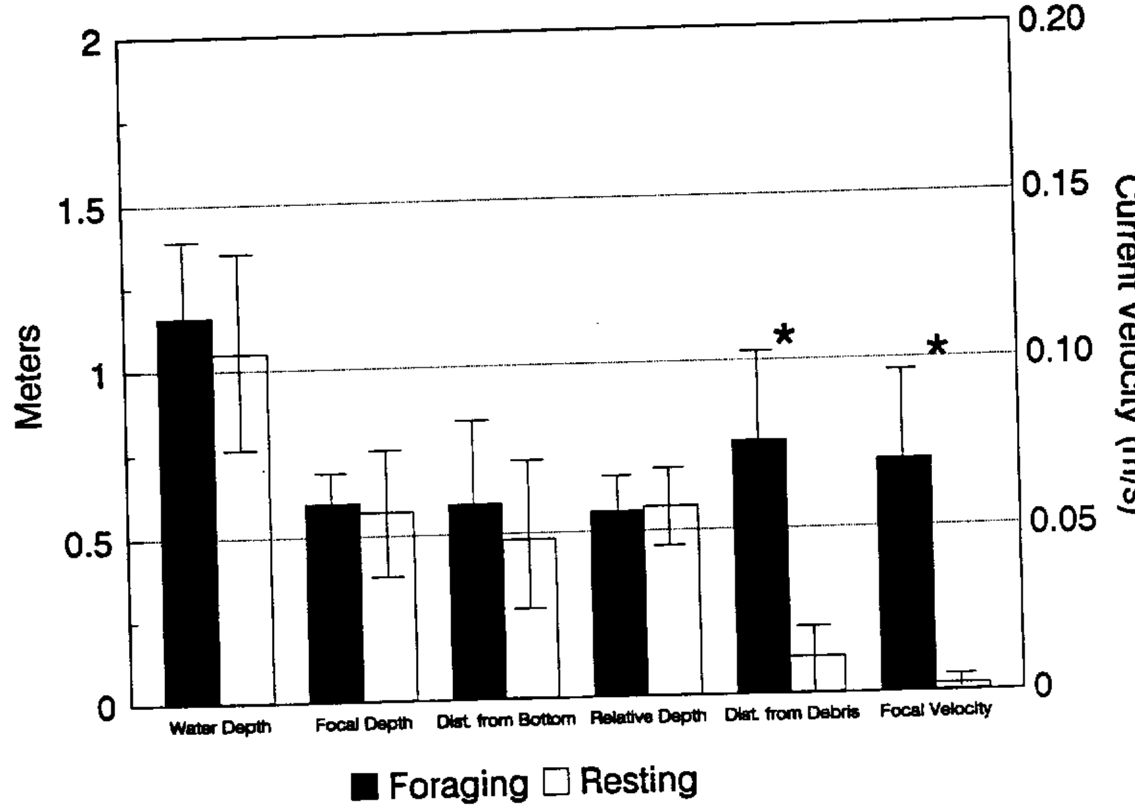

Figure 2. Mean (+/- 2 SE) water depth, focal depth, distance from bottom, distance from debris, relative depth, and focal current velocity selected by groups of foraging and resting juvenile coho salmon in the mainstem Clearwater River during 1992. All the variables except focal velocity refer to the Y-axis on the left. Focal velocities are list on the Y-axis on the right. Groups of bars for microhabitat variables marked with an asterisk (*) are significantly different (Two-way ANOVA: $P<0.05$).

Table 4. Mean focal velocity, focal depth, relative depth, and distance to bottom (September) used by juvenile coho salmon from foraging and resting groups in the mainstem Clearwater River during 1993. Results from the two-way ANOVA evaluating the effect of group (foraging and resting) and habitat (Table 5) on habitat selection variables are also included.

	Foraging Group (F)			Resting Group (R)				
Variable	n	Mean	SD	n	Mean	SD	Results	*P*
Focal Velocity (m/s)	55	0.0673	0.06124	20	0.0035	0.01349	F>R	0.0001
Focal Depth (m)	55	0.55	0.223	20	0.38	0.143	F>R	0.0138
Relative Depth	55	0.64	0.198	19	0.58	0.219	F>R	0.0031
Distance to Bottom (September)	19	0.27	0.238	6	0.24	0.092	F=R	0.5098

Table 5. Mean focal velocity, focal depth, relative depth, and distance to bottom (September) selected by juvenile coho salmon in different river habitat types during 1993. Results from the two-way ANOVA evaluating the effect of group (Table 4) and habitat (pool, glide, riffle) on habitat selection variables also is included.

	Pool (P)			Glide (G)			Riffle (R)						
Variable	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*	Tukey Results		
Focal Vel. (m/s)	19	0.048	0.0449	28	0.050	0.0665	28	0.052	0.0638	0.7810	----	----	----
Focal Depth (m)	19	0.67	0.226	28	0.53	0.215	28	0.37	0.106	0.0005	P>R <0.001	P>G 0.0154	G>R 0.0033
Relative Depth	19	0.51	0.215	28	0.60	0.209	27	0.72	0.143	0.0004	R>P 0.0027	R=G 0.0942	P=G 0.2374
Distance to Bottom (Sept.)	6	0.43	0.262	8	0.29	0.238	11	0.15	0.043	0.0319	P>R 0.0268	P=G 0.4101	G=R 0.3104

Table 6. Mean water depth, distance from bottom (August), and distance to debris selected by foraging (F) and resting (R) coho salmon rearing in pools, glides, and riffles during 1993.

		Foraging (F)			Resting (R)				
Variable	Habitat	n	Mean	SD	n	Mean	SD	Results	P^1
Water Depth (m)	Pool	16	1.36	0.678	3	2.28	0.075	N/A[2]	----
	Glide	21	0.98	0.284	7	0.72	0.133	F>R	0.0275
	Riffle	18	0.56	0.115	10	0.45	0.076	F>R	0.0133
Distance from Bottom (m) (August)	Pool	10	0.84	0.651	3	1.73	0.179	N/A[2]	----
	Glide	15	0.46	0.272	5	0.29	0.121	F=R	0.1905
	Riffle	11	0.15	0.119	6	0.14	0.036	F=R	0.8540
Distance from Debris (m)	Pool	15	0.73	0.856	3	0.41	0.352	N/A[2]	----
	Glide	21	1.51	1.393	7	0.18	0.256	F>R	0.0003
	Riffle	18	0.46	0.609	10	2.19	1.813	R>F	0.0147

[1]Results from t-test.
[2]Insufficient replications for statistical analysis.

Microhabitat use of resting coho salmon was influenced by river habitat type (Table 7). Focal positions used by resting in pools were located in deeper water than those in glides or riffles and in deeper water in glides than riffles (Table 7). Focal positions of resting coho salmon were farther from the bottom in pools than in glides or riffles. Resting fish selected focal positions farther from woody debris cover in riffles than in glides, but no difference was observed in pools versus glides or pools versus riffles. Resting coho salmon in riffles and glides selected greater relative depths (water depth/focal depth) than those in pools. Resting coho salmon in different habitats did not use significantly different focal velocities or focal depths (Table 7). However, the power of these tests was low (focal velocity: <0.20; focal depth: 0.35).

Foraging coho salmon displaying different individual behaviors (dominant, subdominant, and floater) used focal positions with similar microhabitat features (Table 8). No significant differences were observed in any of the microhabitat variables among dominant, subdominant, and floater foraging fish. Floaters were normally in deeper water and further from the bottom, however, these differences were not significant. There was insufficient replication to compare the distance from bottom selected by dominant ($n=2$), subdominant, and floater ($n=1$) fish. A significant interaction existed between the factors (individual class and habitat type) for the variable distance from bottom during August (two-way ANOVA: $P=0.0182$). This required that the comparisons of distance of focal positions from the bottom (August) for each habitat type be compared separately for each individual class. However, there were too few observations for this comparison.

Foraging coho salmon rearing in different habitats occupied focal positions which differed in several of the measured microhabitat variables (Table 9). Foraging coho salmon occupied deeper water in pools than in glides and riffles, and occupied deeper water in glides than in riffles (Table 9). Foraging coho salmon used focal positions twice as far from woody debris in glides than in pools and riffles. Focal positions occupied by foraging fish were deeper in pools than in glides and riffles, but the difference was only significant between pools and riffles. No difference was observed in the distance focal positions used by foraging fish were located from the bottom during September. The comparison of distance to the bottom selected by foraging coho salmon in different habitats during August was completed separately for each individual class, since the interaction between these two factors was significant (two-way ANOVA: $P=0.0182$). However, there was only sufficient data to complete this analysis for subdominant foraging fish. Subdominant foraging fish selected focal positions farther from the bottom in pools than riffles during August.

Table 7. Mean water depth, focal depth, distance from bottom, relative depth, distance from debris, and focal velocity selected by juvenile coho salmon by individuals from the resting group in different riverine habitats during 1993. Results from the ANOVA and tukey tests (only if the ANOVA was significant) are also presented. (For Tukey Results: P=Pool; G=Glide; R=Riffle).

	Pool (P)			Glide (G)			Riffle (R)						
Variable	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*	Tukey Results		
Water Depth (m)	3	2.28	0.075	7	0.721	0.133	7	0.46	0.084	0.0001	P>G <0.001	P>R <0.001	G>R 0.0012
Distance from Bottom (m)	3	1.73	0.179	7	0.30	0.107	7	0.16	0.045	0.0001	P>G <0.001	P>R <0.001	G=R 0.0530
Distance from Debris (m)	3	0.41	0.352	7	0.18	0.256	7	2.72	1.94	0.0058	R>G 0.0335	R=P 0.0518	P=G >0.50
Focal Velocity (m/s)	3	0	0	7	0.001	0.0038	7	0.009	0.0227	0.5997	----	----	----
Focal Depth (m)	3	0.55	0.104	7	0.42	0.147	7	0.33	0.108	0.0748	----	----	----
Relative Depth	3	0.24	0.055	7	0.57	0.141	7	0.73	0.209	0.0003[3]	R>P <0.001	G>P 0.0015	R=G 0.5230

Table 8. Mean water depth, focal depth, distance from bottom, relative depth, distance from debris, and focal velocity of juvenile coho salmon from foraging groups in different individual classes (dominant, subdominant, floater) during 1993. Results of the two-way ANOVA evaluating the two factors (individual class of foraging group) and habitat type (Table 9) comparisons also are provided.

	Dominant			Subdominant			Floater			
Variable	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*
Water Depth (m)	7	0.71	0.294	38	0.98	0.499	7	1.08	0.701	0.7109
Distance from Bottom (m) (September)	2	0.12	0.042	14	0.29	0.263	1	0.49	----	N/A
Distance from Debris (m)	7	1.13	1.381	38	0.92	1.168	6	1.38	0.468	0.1230
Focal Velocity (m/s)	7	0.09	0.037	38	0.07	0.063	7	0.02	0.045	0.1068
Focal Depth (m)	7	0.51	0.188	38	0.56	0.243	7	0.58	0.114	0.9864
Relative Depth	7	0.74	0.133	38	0.62	0.215	7	0.63	0.177	0.7382

Table 9. Mean water depth, focal depth, distance from bottom, relative depth, distance from debris, and focal velocity of juvenile coho salmon from foraging groups rearing in different riverine habitat during 1993. Results from the two-way ANOVA using the two factors individual foraging group class (Table 8) and habitat type (pool, glide, riffle) are also included.

	Pool (P)			Glide (G)			Riffle (R)						
Variable	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*	Tukey Results		
Water Depth (m)	16	1.36	0.678	20	0.95	0.237	16	0.57	0.120	0.0015	P>G 0.0128	P>R <0.001	G>R 0.0226
Distance from Bottom (m) (Aug.)[1]	7	0.86	0.591	9	0.48	0.282	8	0.16	0.135	0.0055	P>R 0.0045	P=G 0.1310	G=R 0.2087
Distance from Bottom (m) (Sept.)	6	0.43	0.262	6	0.27	0.276	5	0.11	0.025	0.2615	----	----	----
Distance from Debris (m)	15	0.73	0.856	20	1.59	1.384	16	0.52	0.623	0.0109	G>P 0.0490	G>R 0.0097	P=R >0.500
Focal Velocity (m/s)	16	0.06	0.043	20	0.06	0.069	16	0.09	0.066	0.7878	----	----	----
Focal Depth (m)	16	0.69	0.237	20	0.56	0.223	16	0.42	0.093	0.0402	P>R 0.0030	P=G 0.1766	G=R 0.1320
Relative Depth	16	0.56	0.196	20	0.61	0.232	16	0.75	0.109	0.1310	----	----	----

[1]Subdominant fish only

Behavior

1992

Behavioral observations collected by the two observers during 1992 showed significant differences (Appendix A) for the variables surface forage attempts (t-test: $P=0.0154$), total forage attempts (t-test: $P=0.0196$), attacks (t-test: $P=0.0032$), and nips by fish in the foraging group (t-test: $P=0.0460$), wanders by fish from both the foraging (t-test: $P=0.0001$) and resting groups (t-test: $P=0.0289$), and chase behavior by resting fish (t-test: $P=0.0369$). Data for these variables were analyzed separately for each observer.

Juvenile coho salmon from foraging groups foraged more than those from resting groups during 1992 (Figure 3). Foraging fish made more surface, midwater, and total forage attempts than those resting fish, while no difference in the number of bottom foraging attempts was observed between the two groups. Although the two observers observed different numbers of surface and total forage attempts by foraging fish, results of the comparison between foraging and resting fish were consistent (i.e., foraging fish fed more).

Juvenile coho salmon in foraging groups displayed more aggressive behavior than those from resting groups during 1992, although results varied between the two observers (Figure 4). Observer 1 recorded significantly more chase and attack behavior in coho salmon from the foraging group than those from the resting group. Although observer 2 also recorded more chase behavior by foraging fish than resting fish the difference was not statistically significant. Observer 2 did not observe any attack behavior by either behavior group. Observer 2 recorded more nips from juvenile coho salmon in the foraging group than those in resting groups, whereas no difference was recorded by observer 1. Foraging fish made more aggressive displays and total aggressive behavior than those resting fish.

Although foraging fish were more aggressive than resting fish, they did not display more submissive behavior than resting fish (Figure 5). No difference was observed in the number of submissive displays, fleeing activities, hiding activities, or total submissive behaviors recorded for fish from the foraging and resting groups.

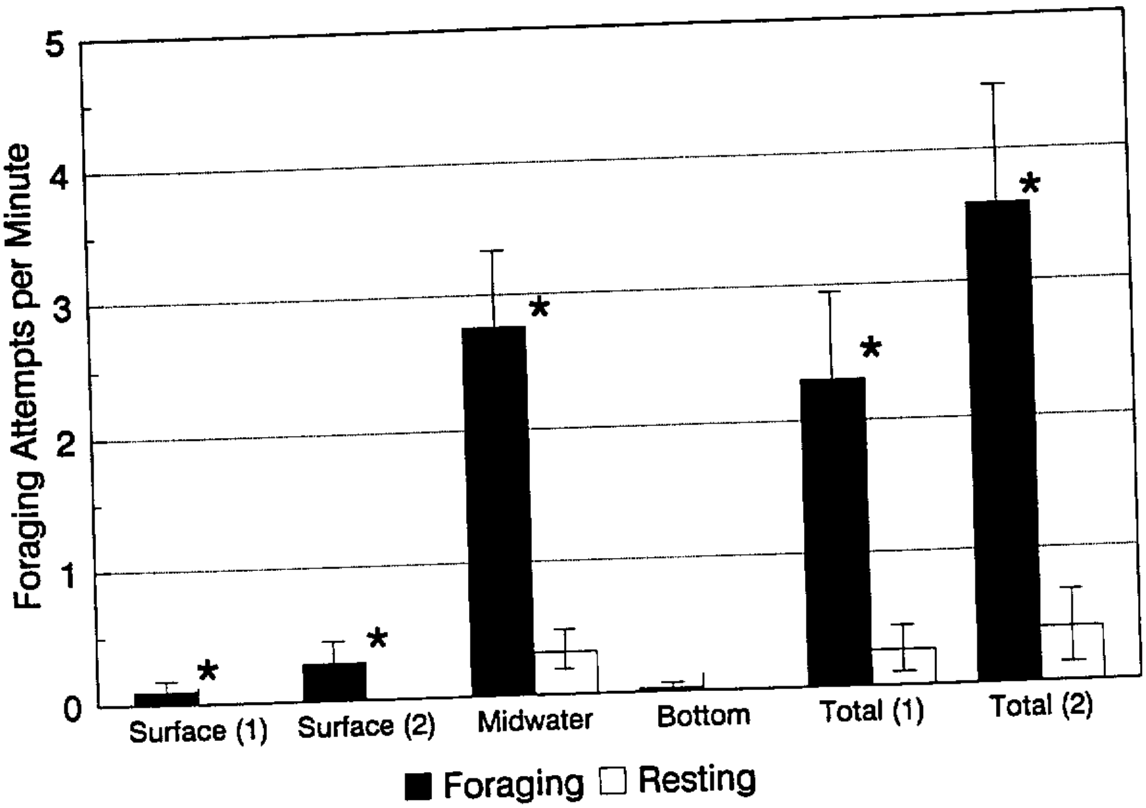

Figure 3. Mean (+/- 2 SE) number of surface, midwater, bottom and total forage attempts (attempts/min.) made by juvenile coho salmon from foraging and resting groups, during 1992. Results obtained by each observer (in parenthesis) are presented for the number of surface and total foraging attempts made, since significant differences existed in the data collected by the two observers. An asterisk (*) above groups of bars indicates significant differences (t-test: $P<0.05$).

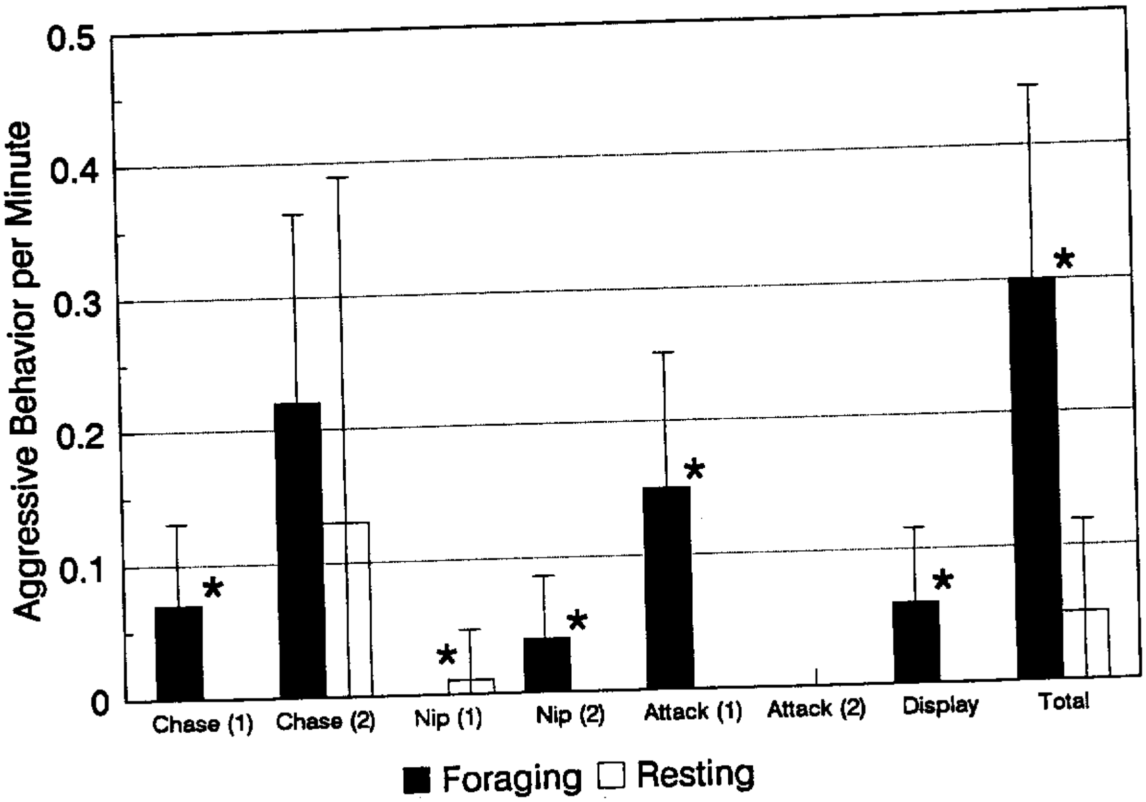

Figure 4. Mean (+/- 2 SE) number of aggressive displays, chases, nips, attacks, and total aggressive behavior per minute observed in juvenile coho salmon from foraging and resting groups during 1992. Mean number of chases, nips and attacks recorded by each observer (in parenthesis) are displayed because significant differences existed between the data collected by the two observers. An asterisk (*) above groups of bars indicates significant differences (t-test: $P<0.05$).

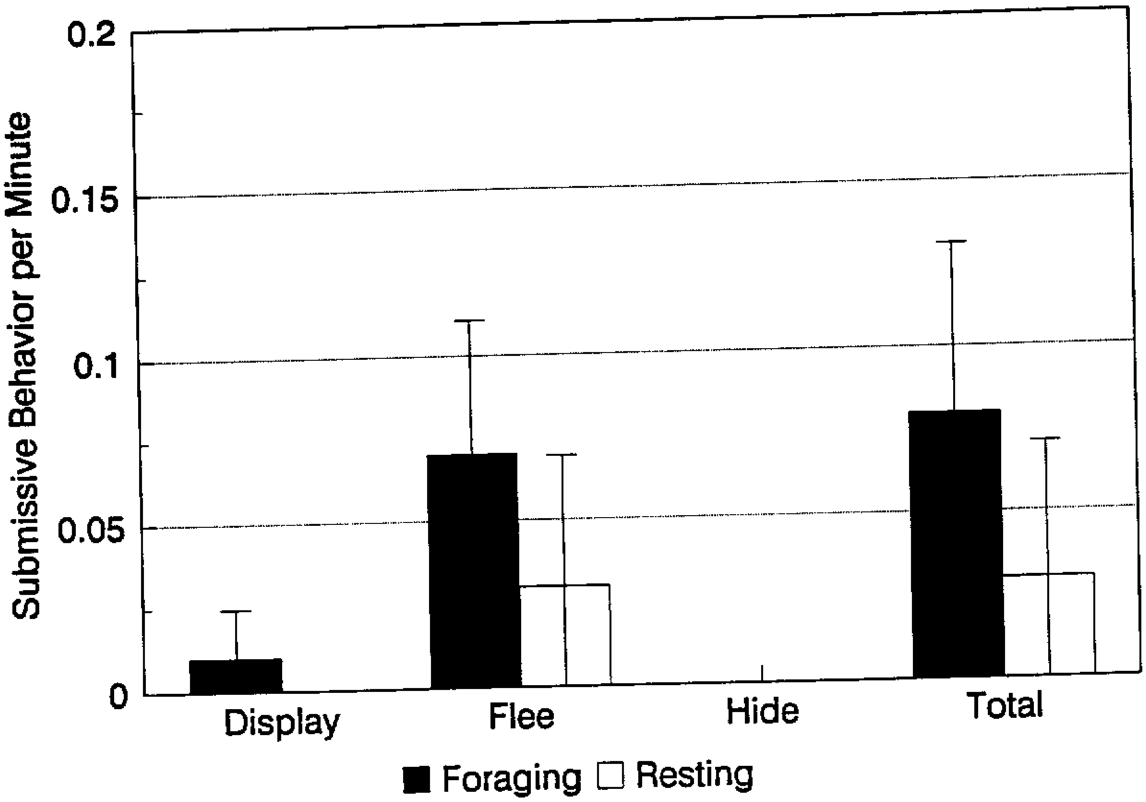

Figure 5. Mean (+/- 2 SE) number of submissive displays, flees, hiding and total submissive behavior per minute observed in juvenile coho salmon from foraging and resting groups during 1992.

No significant (t-test: Observer 1: P=0.8879; Observer 2: P=0.2762) differences in the number of wandering forays per minute were observed between juvenile coho salmon in foraging (Observer 1: Mean=0.31, SD=0.501; Observer 2: Mean=0.01; SD=0.071) and resting groups (Observer 1: Mean=0.30; SD=0.478; Observer 2: Mean=0.05, SD=0.154).

The proportion of coho salmon displaying foraging behavior varied between sampling dates. For example, during the first survey 11 groups of coho salmon totalling over 150 fish were classified as foraging and one group of 8 fish was classified as resting. During the second survey, 4 groups totalling 32 fish were foraging and 10 groups totalling nearly 200 fish were resting. During the third survey, coho salmon were more equally divided (foraging: 5 groups, 32 fish; resting: 2 groups, 47 fish). However, during the final survey, 11 groups totaling nearly 250 fish were foraging, while only 4 groups totalling 40 fish were resting. There were insufficient data to compare the number of coho salmon groups displaying foraging versus resting behavior in relation to time of day or weather conditions.

1993

As expected from their definition, foraging coho salmon foraged more than resting coho salmon (Table 10). However, these differences were significant only for midwater and total forage attempts. Coho salmon from the two behavior groups did not display different foraging intensities during August and September (two-way ANOVA: P=0.2934-0.8423).

Foraging coho salmon were more aggressive than resting fish, however, no difference was detected in the number of submissive behaviors displayed by the two behavior groups (Table 10). Foraging coho made significantly more aggressive displays and displayed more total aggressive behavior than resting individuals. No differences were detected in the frequency of attack, nip, or chase behavior of coho salmon from the two behavior groups. Aggressive behavior did not differ between August and September (two-way ANOVA: P=0.0785-0.9156). No differences were detected in submissive displays, flees, or hiding by coho salmon from the two foraging groups or in the number of submissive behaviors observed between August and September (two-way ANOVA: P=0.2384-7424) (Table 10). Coho salmon wandered more during August than September and those from resting groups wandered more than those from foraging groups (Table 10).

Foraging coho salmon displaying different individual behaviors (dominant, subdominant, floater) showed differences in foraging and aggressive behavior (Table 11). However, these differences were rarely statistically significant due to low replication which results in low statistical power (Table 11). Foraging coho salmon displaying the floater behavior foraged on the surface two to five times more than individuals displaying subdominant and dominant behavior. In contrast, dominant and subdominant foraging fish made twice as many midwater forage attempts and 50% more total forage attempts than floaters. Bottom foraging was similar among individuals displaying dominant, subdominant, and floater behaviors.

Dominant coho salmon displayed more aggressive behavior than those displaying subdominant and floater behaviors, however, these differences were only statistically significant for total aggressive behavior (dominant>subdominant: Tukey: P=0.0173; dominant>floaters: Tukey: P=0.0270). No difference in total aggressive behavior was detected between subdominant and floaters (Tukey: P>0.5000). Although dominant fish made several fold more aggressive displays and attacks than subdominant and floater individuals, these differences were not statistically significant. Subdominant fish were the only ones that displayed chase behavior and it was infrequent.

Submissive behavior was relatively infrequent in foraging coho salmon displaying dominant, subdominant, and floater characteristics (Table 11). Although, relatively large differences existed between these groups of foraging fish, these differences were not statistically significant (Table 11). Dominant fish reacted to aggression with more submissive displays than subdominant and floaters, while subdominant were more likely to flee than dominant and floater individuals. No hiding behavior was observed in foraging coho salmon. Floaters showed fewer total submissive behaviors than subdominant and dominant individuals (Table 11).

Wandering data was analyzed separately for August and September since significant differences in wandering activity existed between months. Floaters wandered more than dominant (Tukey: $P=0.0199$) and subdominant (Tukey: $P=0.0191$) coho salmon during August 1993. No difference was observed between dominans and subdominant (Tukey: $P>0.5000$). There was insufficient observations for statistical analysis for data collected during September 1993.

Table 10. Mean numbers of foraging, aggressive, submissive and wandering behavior displayed per minute by juvenile coho salmon during 1993 (August and September combined). Results of the two-way ANOVA examining the effect of foraging group (foraging and resting) and month (August and September - text) also are provided.

	Foraging group (F)			Resting group (R)				
Behavior	n	Mean	SD	n	Mean	SD	Results	*P*
FORAGING								
Surface	53	0.28	0.944	19	0.11	0.389	F=R	0.6043
Midwater	53	2.97	2.583	19	0.37	0.293	F>R	0.0001
Bottom	53	0.04	0.139	19	0.03	0.138	F=R	0.9197
Total	53	3.30	2.528	19	0.51	0.421	F>R	0.0001
AGGRESSIVE								
Display	53	0.08	0.152	19	0	0	F>R	0.0392
Attack	53	0.09	0.177	19	0.01	0.046	F=R	0.0717
Nip	53	0.004	0.020	19	0	0	F=R	0.2102
Chase	53	0.006	0.0305	19	0.016	0.0502	F=R	0.3454
Total	53	0.18	0.291	19	0.03	0.093	F>R	0.0363
SUBMISSIVE								
Display	53	0.02	0.070	19	0.005	0.023	F=R	0.3372
Flee	53	0.06	0.162	19	0.02	0.069	F=R	0.3843
Hide	53	0	0	19	0	0	F=R	N/A
Total	53	0.08	0.291	19	0.02	0.071	F=R	0.2480
WANDER	53	0.13	0.197	19	0.26	0.312	R>F	0.0325

Table 11. Mean (attempts/min.) foraging, aggressive, submissive, and wandering behavior displayed by dominant, subdominant, and floater coho salmon from the foraging group during 1993. Sample size (n = number of fish observed) and standard deviation for each group and results from the ANOVA are also provided.

	Dominant			Subdominant			Floater			
Behavior	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*
FORAGING										
Surface	7	0.08	0.186	38	0.27	0.992	7	0.54	1.224	0.6759
Midwater	7	3.57	1.778	38	3.14	2.742	7	1.44	2.232	0.2346
Bottom	7	0.01	0.038	38	0.05	0.157	7	0.04	0.113	0.8454
Total	7	3.66	1.822	38	3.46	2.700	7	2.02	2.238	0.3653
AGGRESSIVE										
Display	7	0.16	0.095	38	0.06	0.135	7	0.01	0.038	0.0724
Attack	7	0.20	0.242	38	0.05	0.116	7	0.06	0.151	0.0566
Nip	7	0.02	0.049	38	0.002	0.0114	7	0	0	0.1154
Chase	7	0	0	38	0.008	0.036	7	0	0	0.7219
Total	7	0.38	0.298	38	0.12	0.198	7	0.07	0.189	0.0123
SUBMISSIVE										
Display	7	0.07	0.095	38	0.01	0.068	7	0.01	0.038	0.1372
Flee	7	0.02	0.049	38	0.08	0.187	7	0	0	0.3809
Hide	7	0	0	38	0	0	7	0	0	1.0000
Total	7	0.09	0.131	38	0.09	0.204	7	0.01	0.038	0.5700
Wander (Aug.)	5	0.04	0.089	24	0.12	0.169	6	0.37	0.297	0.0104
Wander (Sept.)	2	0	0	14	0.03	0.058	1	0.67	---	N/A

Juvenile coho salmon from the two behavior groups generally made more forage attempts at introduced than natural woody debris accumulations (Table 12). Juvenile coho salmon rearing at introduced debris accumulations made more than twice as many surface foraging attempts than those at natural debris accumulations, however, these differences were not statistical significant. Foraging fish rearing at introduced debris accumulations made significantly more midwater and total forage attempts than those rearing at natural debris accumulations. In contrast, resting fish made similar numbers of midwater and total forage attempts at introduced and natural debris accumulations. Data for foraging and resting groups were analyzed separately for midwater and total forage attempts since significant differences were observed in foraging intensities among the two groups for these variables (Table 10). Foraging and resting fish made more bottom forage attempts at natural debris accumulations than those rearing at introduced debris accumulations. However, these differences were not significant (Table 12).

Juvenile coho salmon from foraging and resting groups displayed differing levels of foraging activity depending on riverine habitat (Table 13). Data for foraging and resting fish were analyzed separately for midwater and total forage attempts since significant differences were observed among these behavior groups for these foraging variables (Table 10). Foraging coho salmon made more midwater and total foraging attempts in pools and rifles than in glides. Results from the two-way ANOVA indicated significant differences existed among midwater and total forage attempts made by foraging fish in these different habitats (Table 13). However, post-test pair-wise comparisons using the Tukey test failed to detect significant differences (Table 13). Resting fish made more midwater forage attempts in glides than riffles. No significant differences in total foraging activity was observed in resting fish rearing in different river habitat types. Foraging and resting coho salmon foraged on the bottom more often in riffles than in glides and pools. No difference in surface foraging activity of foraging and resting fish was observed among different riverine habitat types (Table 13).

No significant differences in the levels of aggressive behavior for foraging and resting fish rearing at introduced and natural debris accumulations (Table 12) or rearing in different habitat types was observed (Table 13). Data for aggressive displays and total aggressive behavior were analyzed separately by behavior group (foraging and resting) because differences were observed between these two groups for these variables (Table 10). Total aggressive behavior for foraging fish also was analyzed separately for each individual class (dominant, subdominant, floater) because differences had been observed between these groups (Table 11). However there were insufficient sample sizes ($n=7$) to complete statistical analysis for dominant and floater classes. Therefore, only data for the subdominant class was used.

Juvenile coho salmon in riffles made more total submissive behavior displays than those in pools (Tukey: $P=0.0387$) or glides but no differences were observed between pools and glides (Table 13). However, no differences were observed in individual submissive behaviors (i.e., display, flee, etc.) displayed by juvenile coho salmon from different habitat types. No differences in submissive behavior were observed in juvenile coho salmon rearing at different types of woody debris accumulations (Table 12).

There was insufficient sample sizes to complete statistical testing of wandering behavior of coho salmon rearing at different types of debris accumulations and river habitats. Significant differences were detected in the mean number of wandering behaviors displayed by juvenile coho salmon between August and September so the data for each month were analyzed separately. Differences also existed between foraging and resting groups (Table 10) and between the individual classes within the foraging group (Table 11). This would require each of these comparisons be completed separately for each behavior group and individual class (foraging group). However, there were insufficient sample sizes in these groups to complete meaningful statistical tests. The data are for wandering behavior for each month is listed in Tables 6.12 and 6.13.

Foraging type and resting type coho salmon made more forage attempts at midwater locations than the surface or bottom locations (Figure 6). No difference was observed between surface and bottom foraging attempts for either foraging group. Foraging fish displaying dominant (Mean=1.22, SD=1.962, n=21), subdominant (Mean=1.15, SD=2.188, n=114), and floater (Mean=0.67, SD=1.517, n=21) strategies did not show significant differences (two-way ANOVA: $P=0.4182$) in foraging behavior.

Significant differences in the frequency of different types of aggressive behavior were observed in dominant and subdominant foraging coho salmon but not floaters (foraging group) or fish from the resting group (Figure 7). Dominant fish were more likely to attack opponents than chase them, while subdominant fish were more likely to display to an opponent than nip them. No other differences were observed between any combination of aggressive behaviors by dominant and subdominant coho salmon. The comparison of aggressive behavior displayed by foraging fish was completed separately for each individual class because a significant interaction (two-way ANOVA: $P=0.0896$) was detected between individual class and the type of aggressive behavior displayed.

No differences were detected in the type of submissive behavior displayed by juvenile coho salmon from either the foraging or resting group or from the different individual classes (dominant, subdominant, floater) of the foraging group (Figure 8).

Table 12. Mean number (attempts/min.) of foraging, aggressive, submissive, and wandering behavior displayed by juvenile coho salmon rearing at different types of woody debris accumulations during 1993. When significant differences existed between behavior groups, data for each is displayed, otherwise the data for the two foraging groups are combined. Results of the two-way ANOVA for the factor debris type (introduced and natural) are also given. Results for the second factor (habitat type) are given in Table 13.

	Introduced (I)			Natural (N)				
Behavior	n	Mean	SD	n	Mean	SD	Result	*P*
FORAGING BEHAVIOR								
Surface	23	0.44	1.258	50	0.14	0.519	I=N	0.3020
Midwater (foraging group)	19	3.25	3.549	34	2.82	1.892	I>N	0.0187
Midwater (resting group)	3	0.41	0.320	16	0.36	0.298	I=N	0.7372
Bottom	23	0.004	0.0209	50	0.05	0.163	I=N	0.1323
Total (foraging group)	19	3.79	3.444	34	3.02	1.839	I>N	0.0069
Total (resting group)	3	0.41	0.320	16	0.53	0.444	I=N	0.8582
AGGRESSIVE BEHAVIOR								
Display (foraging group)	19	0.06	0.165	34	0.09	0.145	I=N	0.5246
Display (resting group)	3	0	0	16	0	0	I=N	N/A
Attack	23	0.05	0.174	50	0.07	0.149	I=N	0.7595
Nip	23	0	0	50	0.004	0.0207	I=N	1.0000
Chase	23	0	0	50	0.01	0.044	I=N	1.0000
Total (foraging group) (subdominant)	13	0.04	0.084	25	0.17	0.227	I=N	0.0800
Total (resting group)	3	0	0	16	0.03	0.102	I=N	1.0000
SUBMISSIVE BEHAVIOR								
Display	23	0.01	0.042	50	0.02	0.068	I=N	0.9635
Flee	23	0	0	50	0.07	0.170	I=N	0.6084
Hide	23	0	0	50	0	0	I=N	N/A
Total	23	0.01	0.042	50	0.09	0.186	I=N	0.6527
WANDER BEHAVIOR								
August	13	0.13	0.173	34	0.23	0.288	N/A	N/A
September	10	0.12	0.205	16	0.06	0.119	N/A	N/A

Table 13. Mean number (attempts/min.) of foraging, aggressive, submissive, and wandering behavior displayed by juvenile coho salmon rearing at different river habitat types during 1993. When significant differences existed between behavior groups, data for each is displayed, otherwise the data for the two behavior groups are combined. Results of the two-way ANOVA for the factor habitat type (pool, glide, riffle) are also given. Results for the second factor (debris type) are given in table 12).

	Pool (P)			Glide (G)			Riffle (R)						
Behavior	n	Mean	SD	n	Mean	SD	n	Mean	SD	*P*	Tukey Results		
FORAGING BEHAVIOR													
Surface	20	0	0	27	0.40	1.163	26	0.24	0.708	0.2805			
Midwater (foraging group)	16	3.40	2.672	21	2.22	2.808	16	3.53	2.041	0.0251	R=P >0.50	R=G 0.2647	P=G 0.3453
Midwater (resting group)	4	0.31	0.331	5	0.69	0.175	10	0.24	0.211	0.0391	G>R 0.0108	G=P 0.0808	P=R >0.50
Bottom	20	0	0	27	0.004	0.0173	26	0.11	0.216	0.0193	R>G 0.0193	R>P 0.0246	G=P >0.50
Total (foraging group)	16	3.40	2.672	21	2.74	2.873	16	3.92	1.773	0.0253	R=P >0.50	R=G 0.3246	P=G >0.50
Total (resting group)	4	0.31	0.331	5	0.69	0.175	10	0.51	0.519	0.6583			
AGGRESSIVE BEHAVIOR													
Display (foraging group)	16	0.06	0.114	21	0.07	0.160	16	0.119	0.176	0.5700			
Display (resting group)	4	0	0	5	0	0	10	0	0	N/A			
Attack	20	0.06	0.115	27	0.06	0.172	26	0.08	0.170	0.9451			

Table 13. (cont.)

Behavior	Pool (P) n	Pool (P) Mean	Pool (P) SD	Glide (G) n	Glide (G) Mean	Glide (G) SD	Riffle (R) n	Riffle (R) Mean	Riffle (R) SD	*P*	Tukey Results		
Nip	20	0	0	27	0	0	26	0.008	0.0285	0.2991			
Chase	20	0	0	27	0.007	0.039	26	0.02	0.046	0.2991			
Total (foraging group) (subdominant)	12	0.14	0.196	15	0.06	0.115	11	0.19	0.271	0.8543			
Total (resting group)	4	0	0	5	0	0	10	0.05	0.127	1.000			
SUBMISSIVE BEHAVIOR													
Display	20	0	0	27	0.01	0.042	26	0.04	0.091	0.1632			
Flee	20	0.03	0.114	27	0	0	26	0.11	0.207	0.0911			
Hide	20	0	0	27	0	0	26	0	0	N/A			
Total	20	0.03	0.114	27	0.01	0.042	26	0.15	0.227	0.0290	R>P 0.0387	R>G 0.0059	P=G >0.50
WANDERING BEHAVIOR													
Wander (Aug.)	12	0.17	0.326	18	0.22	0.236	17	0.21	0.257	N/A			
Wander (Sept.)	8	0.10	0.233	9	0.06	0.069	9	0.10	0.150	N/A			

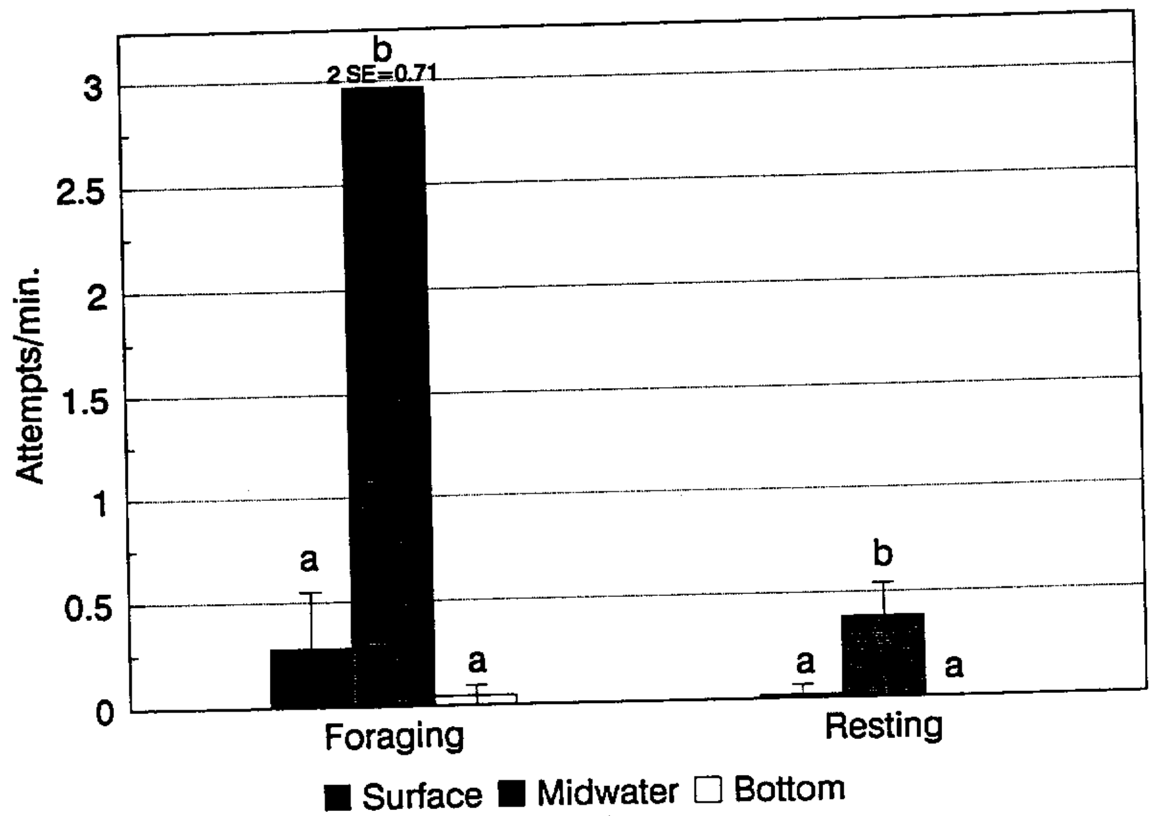

Figure 6. Mean (+/- 2 SE) surface, midwater, and bottom forage attempts (attempts/min.) by juvenile coho salmon from the foraging and resting group during 1993. For each group, bars with different letters are significantly different (Two-way ANOVA (foraging group), ANOVA (resting group), and Tukey: $P<0.05$).

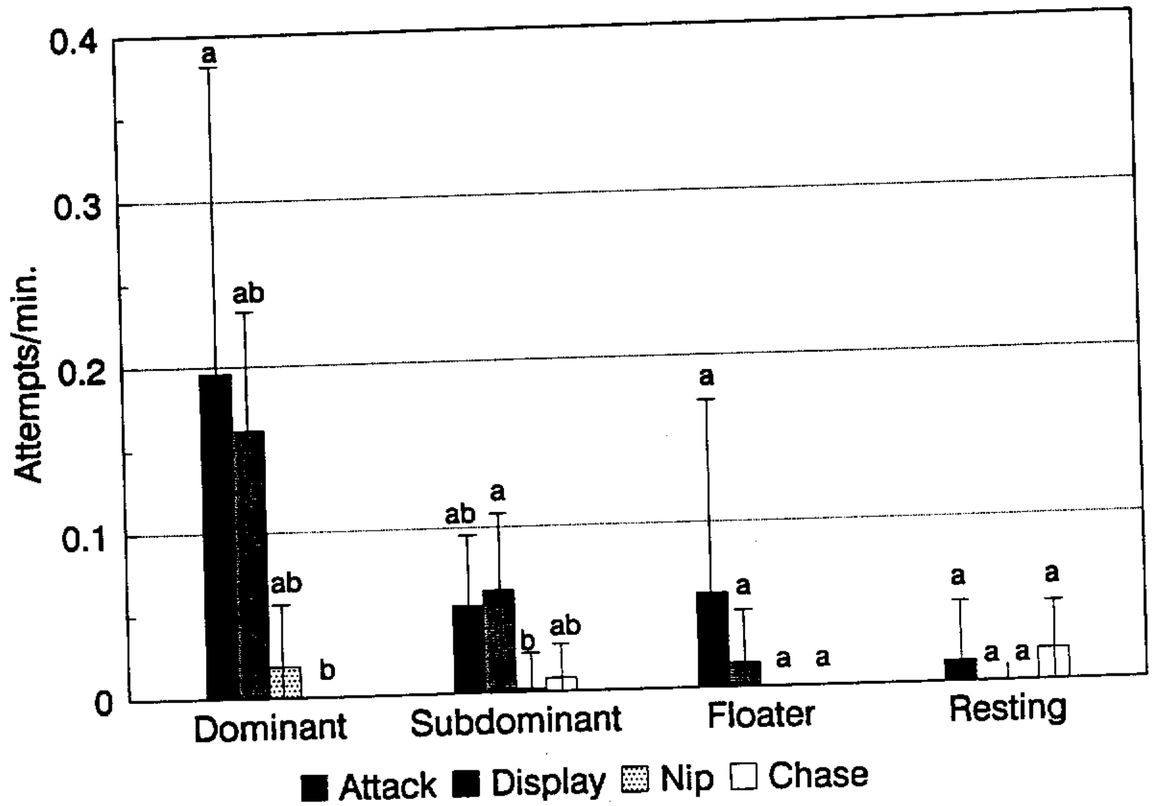

Figure 7. Mean (+/- 2 SE) attack, display, nip, and chase aggressive behavior displayed (attempts/min.) by juvenile coho salmon from the dominant, subdominant, and floater behavior classes of the foraging group, and individuals from the resting group during 1993. For each group, bars with different letters are significantly different (ANOVA and Tukey: $P<0.05$).

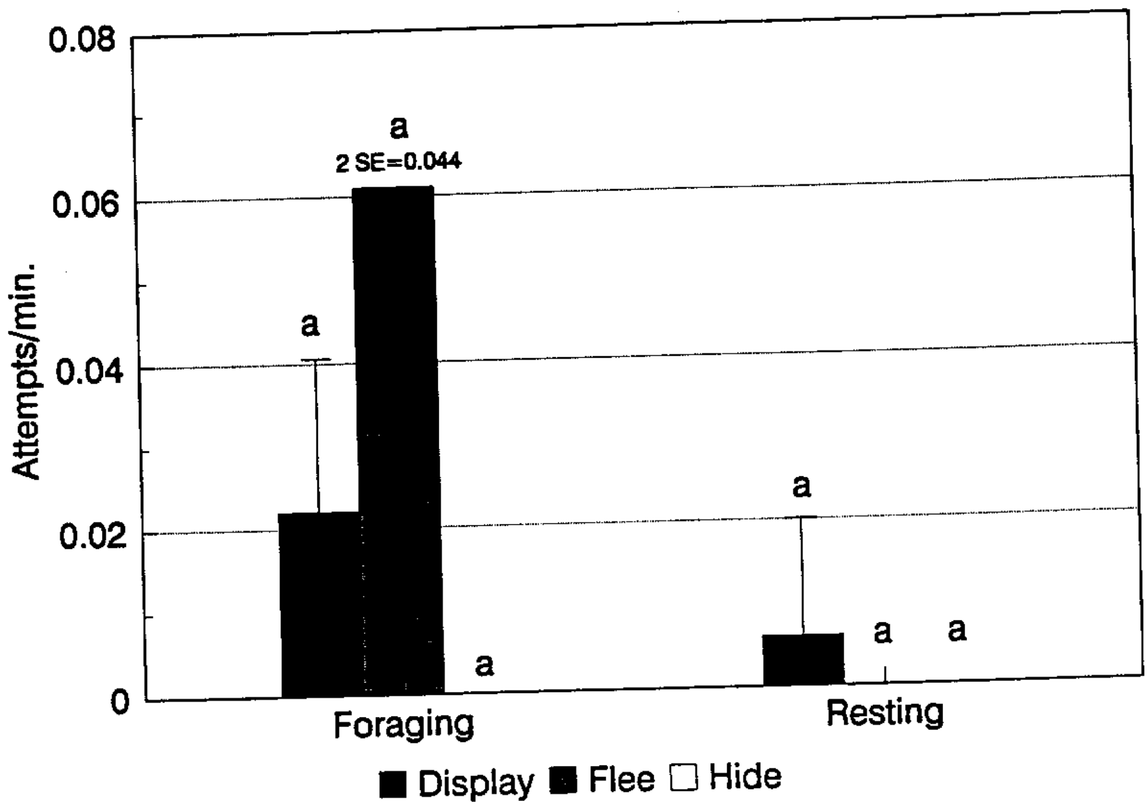

Figure 8. Mean (+/- 2 SE) submissive behavior displays, flees, and nips displayed (attempts/min.) by juvenile coho salmon from the foraging and resting groups during 1993. For each group, bars with different letters are significantly different (Two-way ANOVA (foraging group), ANOVA (resting group) and Tukey: $P<0.05$).

Movement

Of the 194 fish marked between 26 July and 2 August, 60 separate individuals were observed between 5 August and 18 August and 34 were observed between 13 September and 24 September. The determination of marked fish observed during snorkeling observations is somewhat suspect. Of 26 marked fish captured for growth evaluation, 5 had been misidentified by the snorkeler. Errors occurred almost exclusively between fish marked with the colors blue and green, and white and yellow. Since some marks may have been misidentified movement information obtained by snorkeling is not presented. Thus, only movement information from fish actually caught during beach and purse seining is reported.

Twenty-eight fish marked during 26 July and 2 August were recaptured between 13 September and 24 September. Fifteen (53.6%) were captured in the station in which they were marked, while the remaining 13 were captured elsewhere. Three of these 13 fish had moved upstream approximately 100 to 200 meters through a riffle with currents exceeding 0.8 m/s. The 10 other fish had moved downstream: four had moved 20 m to 1.5 km, two between 1.5-3.0 km, and four between 3.0-9 km. Six of the fish occupied different habitat types from their original station. Two moved from pools to glides, and one each moved from a glide to a riffle, glide to pool, riffle to glide, and pool to riffle.

Growth

Due to the extensive movement of juveniles, comparisons of population growth rates of coho salmon from woody debris accumulations located in different riverine habitat types or from different station types would be invalid and therefore were not completed. Thus, comparisons of fish size and growth were completed using only data from marked fish caught at the same station where they were marked. The mean weight of fish marked (5.5 g, SD=1.49) at marking stations was greater than unmarked fish (5.0 g, SD=1.57) from the same station (two-way ANOVA: P=0.0001). For this reason a nested ANOVA (stations nested) was used to compare coho salmon weights from different stations types (introduced and natural) and habitat types (pool, riffle, glide). There was no difference (nested ANOVA: P=0.1244) in the weight of juvenile coho salmon from introduced (Mean=5.4, SD=1.35) and natural debris (Mean=5.1, SD=1.69) accumulations at the time of marking so the data was combined. Coho salmon in pools (Mean = 5.6, SD = 1.52) in late July and early August weighed more than those in glides (Mean = 5.1, SD = 1.31; Tukey: P=0.0040) and riffles (Mean = 4.5, SD = 2.05; Tukey: P<0.001), while no difference was found between weights of juvenile coho salmon rearing in glides and riffles (Tukey: P=0.0640).

Marked fish averaged 75.2 mm (SD=6.27) and 5.3 g (SD=1.41) during late July when they were marked. Marked fish recaptured in mid-September averaged 74.5 mm (SD = 5.96) and 5.2 g

(SD = 1.32) during late July and 89.8 mm (SD=7.15) and 9.0 g (SD=2.12) in mid September. Specific growth rates (%/day) of the fish did not differ (t-test: $P=0.6922$) between introduced (Mean=1.1%/day, SD=0.13) and natural (Mean=1.0%/day, SD=0.08) woody debris accumulations. There was insufficient sample size to compare the growth rate of coho salmon from foraging and resting groups (n=2), or coho salmon rearing in different habitats.

Stomach Analysis

Eighteen marked juvenile coho salmon were caught following the final observation period in September. Of the eighteen, two were from the resting group and two were from unknown behavior groups, since they were not observed during snorkeling. The remaining 14 fish were from the foraging group. This small sample size precluded statistical analysis of this data set, to compare stomach contents of foraging and resting groups, or of coho from different habitat types. Damp weight of stomach contents ranged from 0.0 to 0.394 g (Mean=0.069 g, SD=0.0925), with the two groups from the resting group having stomach contents weighing 0.011 g and 0.085 g, which was within the range of the foraging group. The most common items were exuviae (aquatic insect exoskeletons), ephemeroptera, adult terrestrial insects, chironomidae larvae, and elmidae larvae. Other common invertebrates found included; chironomidae (pupae and adults), trichoptera, plecoptera, other diptera (larvae, adults), hymenoptera, and aracnidae.

DISCUSSION

Two distinct behavior classifications were observed in juvenile coho salmon rearing in the mainstem Clearwater River. Foraging and resting groups of coho salmon showed differences in habitat use and intensity of foraging and aggressive behavior. Foraging groups occupied focal positions with greater current velocities, water depth, and relative depths than resting groups. They also selected focal positions farther from woody debris cover than resting fish in glides, but were closer to woody debris in riffles. Foraging coho salmon generally fed more actively than those from resting groups, primarily foraging in midwater rather than the surface or bottom. Foraging fish were also more aggressive than resting fish with the most noted difference in the frequency of lateral displays. Focal velocities and location of focal positions, relative to depth occupied by juvenile coho salmon in the mainstem Clearwater River were similar to what would have been inferred from other work on coho salmon microhabitat use in small streams (e.g., Dolloff and Reeves 1990; Bugert et al. 1991; Nielsen 1992). Behavior also was similar to that described for coho salmon in small streams (Nielsen 1992).

Although only habitat use was measured in the present study, I assume that much of the information presented also represents habitat preferences. Habitat preferences are normally determined by comparing habitat use to habitat availability, so that habitat selection data can be adjusted according to habitat availability (Bovee 1986). Although habitat availability was not measured in the present study, habitat use was monitored over a wide range of habitat types. A broad range of water depths (0-8 m) and current velocities (0-3.0 m/s) were available for use at the stations we sampled and they included the most extreme cases available throughout most of the river. Areas both with and without woody debris were available at the stations we monitored. Therefore, it seems reasonable to conclude that information presented here represents preferred microhabitat use of juvenile coho salmon in the mainstem Clearwater River given the potential predators and competitors present in this system.

Coho salmon from the mainstem Clearwater River generally used focal velocities (0-0.09 m/s) similar to those reported in the literature (e.g., Sheppard and Johnson 1985; Dolloff and Reeves 1990; Nielsen 1992). Different behavioral groups occupied a wide range of current velocities. Foraging groups used focal positions with much faster current velocities (0.07 m/s) than resting groups (0.004 m/s). Foraging fish also selected a wide range of focal velocities depending on foraging position and behavior (dominant: 0.09 m/s > subdominant: 0.07 m/s > floaters: 0.02 m/s). Differences in focal velocities selected by juvenile coho salmon displaying dominant, subdominant, and floater foraging behaviors have been observed in small streams (Nielsen 1992, 1994). Focal velocities selected by dominant, subdominant, and floater coho salmon in the mainstem Clearwater River were similar to those reported by Nielsen (1992) for a much smaller stream.

Juvenile coho salmon in the mainstem Clearwater River selected midwater positions within the water column as was observed in small streams (Dolloff and Reeves 1990; Bugert et al. 1991). Although focal depths and water depths were much deeper than those normally reported in small streams (Dolloff and Reeves 1990; Bugert et al. 1991), these differences were likely the result of the greater depths associated with the larger system. The differences observed in focal depth and water depth at the focal position of coho salmon rearing in different habitat types are assumed to be the result of physical differences between the habitats themselves. The greater relative depth used by foraging fish may have been related to the greater distance these fish were from woody debris. Coho salmon in southern Alaska occupied greater relative depths in pools lacking in-stream or riparian cover than those with in-stream or riparian cover (Bugert et al. 1991).

Juvenile coho salmon in the mainstem Clearwater River did not directly orient to woody debris cover. These results support the finding of Fausch (1993) but contradict results reported in Peters 1996. These contrasting results are likely the result of habitat selection surveys being completed at different scales. Results presented in this study and by Fausch (1993) were obtained on a microhabitat scale, where habitat variables are measured with reference to the focal position of individual fish. In contrast, results presented in Peters (1996) were obtained at the macrohabitat scale, which examines the relationship between fish densities and general habitat features (i.e., presence of cover, substrate, current velocities). Differences in results from habitat use experiments conducted at different scales indicate that habitat variables influence habitat use differently at different scales. This emphasizes the importance of completing habitat selection studies at an appropriate scale to fully describe the fish/habitat relationship (Bozek and Rahel 1991).

The influence of woody debris cover on the habitat use by salmonids has been the subject of numerous studies (e.g., Wilzbach et al. 1986; Shirvell 1990; Fausch 1993). Numerous factors can influence habitat use with respect to cover including the presence or absence of predators and competitors (Hartman 1965; Bugert and Bjornn 1991; Abrahams and Healey 1993), food supply (Wilzbach et al. 1986), and current velocities (Shirvell 1990, Fausch 1993). Stream dwelling juvenile salmonids must integrate the importance of each of these factors when selecting rearing habitats (Dill and Fraser 1984). The importance given to each of these factors may influence habitat use differently in different habitats and at different scales. At a macrohabitat scale, woody debris may provide protection from predators (Everest and Chapman 1972; Grant and Noakes 1987; Lonzarich and Quinn 1995). However, at a microhabitat scale, direct association with complex woody debris cover may reduce the foraging efficiency of salmonids (Wilzbach 1985). Thus, while macrohabitat use in areas containing woody debris cover may provide security from intermittent predator attacks (macrohabitat importance), focal positions not directly associated with woody debris, providing better foraging opportunities (microhabitat preference), may outweigh the importance of continuous cover from predators. In habitats with current velocities faster than those preferred, juvenile salmonids may select focal positions near woody debris providing refuge from these currents (macro- and microhabitat preference). Protection from these currents may be more important than potential decreases in foraging efficiency resulting from the close association with complex cover in these areas. In these examples, the cover provided by woody debris may be an intermittent requirement during predator attacks or a continuous requirement in areas with extreme current velocities. The observation of coho salmon fleeing into woody debris cover (up to 3 m away) to avoid predators (otter, mergansers, and cutthroat trout) on several occasions during this study supports this concept. Bugert and Bjornn (1991) also observed coho salmon, not directly associated with woody debris, fleeing into woody debris cover in response to predators.

Differences in distance to woody debris cover between resting and foraging groups and between foraging groups in different habitats are likely the result of differences in foraging benefits, refuge from current velocities, and perceived risks of predation associated with these different behaviors and habitats. The relatively close proximity of juvenile coho salmon to woody debris cover in pools suggests that the perceived risks of predation are high, food supplies are not significantly different at differing distances from woody debris, or foraging efficiency is not reduced by complex cover in this habitat. In most cases, current velocities in pools of the Clearwater River are equal to, or less than, the preferred velocities of coho salmon. Thus, woody debris in pools likely does not provide refuge from current velocities on a continuous basis. Large trout were most commonly associated with pool habitats. Pools were also frequented by mergansers, kingfishers, and river otters. However, these terrestrial predators were also present in glides, where foraging coho salmon were generally located farther from woody debris. These differences may be the result of different frequencies of predator presence or food abundance in these habitats. No information is available regarding frequencies of predator presence or food availability in these two habitats. However, food transport should be greater in the faster current velocities associated with glides.

The close proximity of foraging juvenile coho salmon to woody debris in riffles was likely a response to high current velocities (McMahon and Hartman 1989; Shirvell 1990; Fausch 1993). Foraging coho salmon were generally downstream or in current breaks provided by woody debris accumulations. Refuge from fast currents likely was more important than possible reduction in foraging success as a result of woody debris complexity (Wilzbach 1985). Food would be expected to be abundant in riffles due to steady transport in the high currents which may result in higher priority being given to refuge from extreme current velocities.

In contrast to foraging fish, resting fish were closely associated to woody debris in pools and glides, but not in riffles. Differences in distance of focal positions from woody debris may have been related to interspecific competition, food abundance, desire to forage, or willingness to risk predation. Foraging fish displayed more aggressive behavior than resting fish, suggesting that interspecific competition between these groups may have resulted in different distances of focal positions to woody debris cover.

Although food abundance was not measured in the present study, one would expect it to be greater in the faster current areas selected by foraging coho salmon than the slower areas use by resting coho salmon. Assuming competition did not determine habitat use of resting fish, these fish may have a somewhat reduced desire to forage than foraging fish. The different levels of aggressive behavior observed between these two groups may simply be the result of the greater desire of foraging fish to forage, which results in increased aggression towards perceived competitors (Dill and Fraser 1984) than would be the case with resting fish.

Differences in foraging intensity may result from differences in food availability or satiation of fish. If food abundance was reduced during certain periods of the day or the fish became satiated, coho salmon may have used focal positions in slower current velocities near cover. These areas would require less energy to maintain position and would provide better protection from predators (likely important to non-foraging fish).

Stream dwelling salmonids often move from foraging positions to slower waters, apparently as a result of satiation (Bachman 1984; Nielsen 1992). If this were the case for resting fish observed in the Clearwater River, one would expect resting fish to have fuller stomachs than foraging fish. However, the limited stomach samples collected in the present study did not support this conclusion. Both stomach samples from resting coho salmon contained prey weights within the range observed for foraging coho salmon. Twenty-five percent of the sixteen foraging fish sampled had total prey weights greater than one of the resting fish and seventy-five percent of the sixteen foraging fish had total prey weights greater than the second resting fish. These very limited observations suggests that the two resting fish were not satiated. Thus, either food abundance and/or other alteration of foraging desire in foraging fish, both of which may reduce a fish's willingness to risk predation, is responsible for differences in distances of focal positions of foraging and resting fish from woody debris cover. However, since food abundance was not measured in the present study, strong conclusions cannot be drawn.

The classification of foraging coho salmon as dominant, subdominant, and floaters in this study may not accurately reflect all behavior of coho salmon in this study. Wild coho salmon smolts form aggregates near woody debris in the lower reaches of Carnation Creek and its estuary (McMahon and Holtby (1992). Aggregates have been defined by Cunjak and Power (1986) as a close associated group of fish displaying common behavior but lacking the spatial homogeneity and polarity of schooling fish. Coho salmon in the present study seemed to form aggregates in areas with slower currents and with large areas of available space (pools and glides). In areas with faster current velocities and limited habitat availability (riffles and glides) they appear to form hierarchies. However, recognition of the differences between these two groups was not readily apparent until a substantial amount of behavioral data had been collected. It is likely that dominant and subdominant coho salmon observed in pools and glides during the present study represent aggregate coho salmon, while those observed in riffles represent social hierarchies. The separation of these groups cannot be done accurately with the data collected and elimination of data collected prior to the recognition of aggregates would weaken the statistical power of data presented. Some schooling behavior (one group of fish) also was observed during marking surveys used to monitor wall-base channel immigration (Peters 1996).

An understanding of fish behavior is important for successful habitat restoration/enhancement activities. Coho salmon displayed different behavior and these behavioral groups used significantly different habitats in this study. The extent of these differences were somewhat influenced by river habitat type. Habitat rehabilitation/enhancement efforts should be planned to provide rearing areas for all behavioral groups present in the area. Woody debris introductions in the mainstem Clearwater River would provide sufficient habitat for coho salmon in this system. Placement of woody debris should be such that areas on the outer edge and upstream of the woody debris possess current velocities used by foraging groups in the present study, to insure that foraging locations are available. Woody debris placements should also provide areas of slack water within the structure to provide habitat for resting groups of fish.

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APPENDIX A: Comparison of habitat selection and behavioral data collected by the two observers during 1992.

Table A.1. Results of the comparison of coho salmon habitat selection data collected by the two observers during 1992.

Habitat Variable	Class	Observer 1 Mean	Observer 1 SD	Observer 1 n	Observer 2 Mean	Observer 2 SD	Observer 2 n	*P*
Water Depth	Foraging	1.199	0.4581	14	1.126	0.4755	18	0.6640
Water Depth	Resting	1.017	0.4918	12	1.120	0.5188	6	0.6851
Focal Velocity	Foraging	0.0736	0.0858	14	0.0711	0.0605	18	0.9248
Focal Velocity	Resting	0.0025	0.0087	12	0.0	0.0	6	0.4962
Distance to Surface	Foraging	0.5950	0.2173	14	0.6122	0.1840	18	0.8099
Distance to Surface	Resting	0.545	0.2373	12	0.612	0.2629	6	0.5947
Distance to Bottom	Foraging	0.658	0.3858	14	0.533	0.3738	18	0.3618
Distance to Bottom	Resting	0.486	0.3512	12	0.462	0.2726	6	0.8849
Relative Depth	Foraging	0.517	0.1339	14	0.594	0.1738	18	0.1694[a]
Relative Depth	Resting	0.571	0.1483	12	0.555	0.0499	6	0.7209[a]
Distance to Debris	Foraging	0.717	0.6458	14	0.787	0.8321	18	0.7968
Distance to debris	Resting	0.1200	0.1658	12	0.0767	0.1878	6	0.6232

[a]Statistical analysis completed using arcsine transformed data ($x' = \arcsin(x)^{1/2}$)

Table A.2. Results of the comparison of juvenile coho salmon behavior collected by the two different observers during 1992.

		Observer 1			Observer 2			
Behavior	Class	Mean	SD	n	Mean	SD	n	*P*
Surface Foraging	Foraging	0.094	0.2226	48	0.280	0.4755	50	0.0154
Surface Foraging	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Midwater Foraging	Foraging	2.198	2.2043	48	3.290	3.2232	50	0.0541
Midwater Foraging	Resting	0.257	0.5086	37	0.400	0.5758	20	0.3369
Bottom Foraging	Foraging	0.010	0.0722	48	0.020	0.0990	50	0.5865
Bottom Foraging	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Total Foraging	Foraging	2.302	2.1971	48	3.590	3.080	50	0.0196
Total Foraging	Resting	0.257	0.5086	37	0.400	0.5758	20	0.3369
Chase	Foraging	0.073	0.2304	48	0.220	0.4861	50	0.0603
Chase	Resting	0.0	0.0	37	0.125	0.3582	20	0.0369
Attack	Foraging	0.146	0.3414	48	0.0	0.0	50	0.0032
Attack	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Nip	Foraging	0.0	0.0	48	0.040	0.1370	50	0.0460
Nip	Resting	0.014	0.0822	37	0.0	0.0	20	0.4672
Aggressive Display	Foraging	0.021	0.1010	48	0.090	0.3454	50	0.1855
Aggressive Display	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Total Aggression	Foraging	0.240	0.5553	48	0.350	0.7576	50	0.4142
Total Aggression	Resting	0.014	0.0822	37	0.125	0.3582	20	0.0743
Submissive Display	Foraging	0.0	0.0	48	0.020	0.0990	50	0.1648
Submissive Display	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Flee	Foraging	0.083	0.2596	48	0.060	0.1927	50	0.6136
Flee	Resting	0.041	0.1818	37	0.0	0.0	20	0.3249

Table A.2. (cont.)

Behavior	Class	Observer 1			Observer 2			
		Mean	SD	n	Mean	SD	n	*P*
	Foraging	0.0	0.0	48	0.0	0.0	50	1.0000
Hide								
Hide	Resting	0.0	0.0	37	0.0	0.0	20	1.0000
Total Submissive	Foraging	0.083	0.2596	48	0.080	0.2339	50	0.9468
Total Submissive	Resting	0.041	0.1818	37	0.0	0.0	20	0.3249
Wander	Foraging	0.313	0.5013	48	0.010	0.0707	50	0.0001
Wander	Resting	0.297	0.4781	37	0.050	0.1539	20	0.0289

APPENDIX B. **August and September, 1993 habitat selection data.**

Table B.1. Comparison of habitats selected by juvenile coho salmon from different foraging groups during August and September 1993.

Variable	August			September			*P* (t-test)
	Mean	SD	n	Mean	SD	n	
Foraging Group							
Water depth (m)	1.01	0.588	36	0.85	0.314	19	0.1750
Focal depth (m)	0.54	0.219	36	0.58	0.233	19	0.4696
Focal Velocity (m/s)	0.06	0.054	36	0.07	0.074	19	0.6417
Distance to bottom (m)	0.47	0.462	36	0.27	0.238	19	0.0409
Relative Depth[a]	0.60	0.208	36	0.71	0.160	19	0.0555[b]
Distance to debris (m)	0.97	1.162	36	0.90	1.078	18	0.8297
Resting Group							
Water depth (m)	0.92	0.753	14	0.58	0.133	6	0.1156
Focal depth (m)	0.38	0.162	14	0.38	0.096	6	0.9712
Focal Velocity (m/s)	0.004	0.0160	14	0.002	0.0041	6	0.5768
Distance to Bottom (m)	0.53	0.658	14	0.24	0.092	6	0.1286
Relative Depth[a]	0.53	0.191	14	0.69	0.255	6	0.5228[b]
Distance to debris (m)	0.52	0.410	14	2.85	2.212	6	0.0501

[a]Calculated as focal depth/water depth
[b]Statistical analysis completed on arcsine transformed data ($X' = \text{arcsine}(X)^{1/2}$)